American Fern Journal 85(1):1–28 (1995)

Identification of the Juveniles of Some Ferns from Western Amazonia

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In floristic inventories and ecological studies it is often desirable to collect and identify all individuals of the plants involved. This is necessary if the total number of individuals is to be counted, or if the age structures of populations are to be clarified. Identification of juvenile plants in the tropical rain forests is difficult, and ferns are no exception. Both fern floras and monographic treatments concentrate on describing adult plants, and all identification keys are based on adult material. Usually it is even necessary for proper identification that fertile leaves are present. The fertile-sterile leaf dimorphism has been described in detail for those species in which it is found, but differences between juvenile and adult stages have been treated only occasionally. One obvious reason for this is the lack of juvenile collections in herbaria; both general collectors and herbarium curators tend to prefer fertile material.

For a few fern species, the anatomical development of the juveniles has been described in detail (Goebel, 1913, Kato and Iwatsuki, 1985; Knaben, 1948; Orth, 1938; Wagner, 1952a, 1952b, 1952c; White, 1971). The juveniles of *Lomagramma guianensis* have been treated in connection with architectural studies on the species (Gay, 1993), and the juveniles of *Danaea wendlandii* have received attention in population ecological studies (Sharpe and Jernstedt, 1990). Some taxonomical treatments include detailed descriptions of the structure of young leaves, notably the revision of *Lomariopsis* by Holttum (1939) and the revision of *Bolbitis* by Hennipman (1977). Also Tryon and Tryon (1982) and Tryon and Stolze (1989a, 1989b, 1991, 1992, 1993) include occasional comments on juvenile ferns.

However, most of these articles have concentrated on the description of the juvenile development of one or more species with main interest in anatomy or morphology rather than species identification. Also the systematical treatments have either been purely descriptive, or have made comparisons only among species within a single genus. Similarities that exist among juveniles belonging to different genera have never been sorted out.

During this work, ferns have been inventoried in eight sites around Iquitos (for details on methodology and location, see Ruokolainen et al. in press, Tuomisto and Ruokolainen, 1994, Tuomisto and Poulsen, in review). These studies have produced a lot of juvenile material, and it became possible to reconstruct developmental series for most of the species involved.

The present article concentrates on the most difficult group of species, namely

those that have simple leaves when they are young, but produce pinnate leaves when they get older. These species are: *Bolbitis nicotianifolia, Cyclodium meniscioides, Danaea leprieurii, D. nodosa, D. ulei, Lomariopsis nigropaleata, Salpichlaena hookeriana, S. volubilis* and *Thelypteris macrophylla*. Included are also some species that stay simple even at maturity because they can be confused with juveniles of the above-mentioned species: *Asplenium serratum, Campyloneurum phyllitidis, C. repens* and *Elaphoglossum discolor*. Two species that do not have simple leaves are included because they can be confused with intermediate juvenile stages of the first-mentioned species group: *Metaxya rostrata* and *Saccoloma elegans*. This selection of species is by no means exhaustive, and there are several additional species that could be included. However, the available juvenile collections restrict us to these 15 species.

IDENTIFICATION

In most cases rhizomes have important diagnostic characteristics, and many genera and even species can be easily identified on the basis of the rhizome alone. However, we have avoided using rhizome structure as the only diagnostic characteristic in the couplets of the key, because specimens lacking rhizomes are rather abundant in herbaria. For the same reason, the presence or absence of stipules is only used in connection with other features; although in principle a reliable characteristic of the genus *Danaea*, stipules are not always readily visible in juveniles, and are often lacking in carelessly collected adult material. All ferns have very slender rhizomes when small; when rhizome diameters are cited in the text, they always refer to large plants.

Venation is among the most important diagnostic characteristics for species identification. In all descriptions of the venation we use the following terms: "midrib" for the central vein of a simple leaf or pinna, "vein" for the veins emerging from the midrib, and "veinlet" for all smaller veins. All measurements of distances among veins or veinlets are measured in mid-leaf halfway between midrib and the leaf margin.

All characteristics apply to plant material that has been preserved with alcohol prior to drying, unless it is explicitly stated that they refer to fresh material; treatment with alcohol tends to change the colors.

Many of the species change so much during their development that they cannot be keyed out with the same characteristics during all stages. Therefore most species are mentioned more than once in the key. The exceptions are *Bolbitis nicotianifolia, Campyloneurum* spp. and *Thelypteris macrophylla*, which can be identified on the basis of their venation patterns at any stage. Fertile leaves are virtually ignored in the present study, and all characteristics given refer to sterile leaves except in the few cases where it is explicitly stated otherwise.

Most of the voucher specimens studied, and all the ones illustrated, are deposited in the herbarium of the University of Turku (TUR). For the genera *Danaea* and *Salpichlaena*, additional material from the herbaria of the University of Aarhus (AAU), the British Museum (BM), Kew Gardens (K) and the

University of Utrecht (U) has been consulted. Nomenclature is according to Tryon and Stolze (1989a, 1989b, 1991, 1992, 1993) unless stated otherwise.

Key to the Juveniles

1. Veins more than 3 mm apart, connected by veinlets
   2. Petiole indistinct; lamina base long-attenuate; leaves simple
      3. Leaf margin distinctly sinuate; venation irregular and incompletely anastomosing, or with veinlets converging in a sharp angle often uniting in an excurrent veinlet, forming a herring-bone pattern . . . . . *Cyclodium meniscioides* (Fig. 3a)
      3. Leaf margin entire or slightly crenate; veinlets converging in a blunt angle, forming blocky areoles with free included veinlets
         4. Number of included veinlets per areole 2–4; length of internodes less than the diameter of the rhizome . . . . . *Campyloneurum phyllitidis* (Fig. 1c)
         4. Number of included veinlets per areole 2; length of internodes several times the diameter of the rhizome . . . . . *Campyloneurum repens* (Fig. 1d)
   2. Petiole distinct; lamina base obtuse to cuneate or short-attenuate; leaves pinnate or simple
      5. Veinlets forming small cell-like areoles with free included veinlets pointing to various directions . . . . . *Bolbitis nicotianifolia* (Fig. 2a–d)
      5. Veinlets converging in an angle, veinlet pairs often giving rise to free excurrent veinlets always pointing towards the leaf margin
         6. Leafbase cuneate; veinlets curved, forming a herring-bone pattern, many veinlet pairs without excurrent veinlets . . . . . *Cyclodium meniscioides* (Fig. 3b,c)
         6. Leafbase obtuse; veinlets almost straight, forming regularly angular areoles, each veinlet pair with one excurrent veinlet . . . . . *Thelypteris macrophylla* (Fig. 9a,b)
1. Veins less than 2 mm apart, veinlets absent
   7. Leaves simple
      8. Leafbase long-attenuate; petiole absent or less than 1/10 the length of the lamina
         9. Leaves close, in rosette; veins spreading at 30–75° from the midrib . . . . . *Asplenium serratum* (Fig. 1a,b)
         9. Leaves distant along creeping rhizome; veins spreading at 80–90° from the midrib . . . . . *Lomariopsis nigropaleata* (Fig. 6a,b)
      8. Leafbase short-attenuate to cuneate or rounded; petiole more than 1/10 the length of the lamina
         10. Petiole nonalate; leaf apex serrate or with hair-like protrusions
            11. Leaf apex serrate; leaf margin usually the same color as lamina; leaves less than about 30 cm long and 3.5 cm wide . . . . . *Salpichlaena hookeriana* (Fig. 8a)
            11. Leaf apex entire, with hair-like protrusions that do not extend to the green leaf tissue; leaf margin narrowly pale; leaves up to about 60 cm long and 7 cm wide
               12. Leaf margin distinctly cartilaginous; leaf base cuneate to rounded; petiole base slender and curved; stipules absent . . . . . *Salpichlaena volubilis* (Fig. 5d)
               12. Leaf margin not cartilaginous; leaf base short-attenuate; petiole base swollen and straight; stipules present . . . . . *Danaea ulei* (Fig. 5a)
         10. Petiole narrowly alate; leaf apex entire or shallowly crenate
            13. Rhizome upright, cylindrical, or if dorsiventral then very short-creeping and leaves in rosette; stipules present; leaf apex obtuse to acute
               14. Rhizome upright, cylindrical; lamina ovate with acute apex; leaf up to 13 cm long . . . . . *Danaea leprieurii* (Fig. 4c)
               14. Rhizome short-creeping, dorsiventral; lamina orbicular with obtuse apex; leaf up to 4 cm long . . . . . *Danaea nodosa*
            13. Rhizome creeping, dorsiventral; stipules absent; leaf apex acute to cuspidate

15. Leaves lanceolate to elliptic; leaf apex acute to acuminate; veins slightly curved with the convex side towards leaf apex . . . . . *Elaphoglossum discolor* (Fig. 1e)
15. Leaves broadly linear; leaf apex acuminate to cuspidate; veins slightly curved with the concave side towards leaf apex . . . . . *Lomariopsis nigropaleata* (Fig. 6b,c)

7. Leaves pinnate
16. Leaves with three pinnae
17. Base of terminal pinna attenuate, gradually tapering into a narrowly alate rachis; pinna apex entire to shallowly crenate
18. Lateral pinnae alternate; terminal pinna more than 10 cm long; rhizome long-creeping, dorsiventral; stipules absent . . . . *Lomariopsis nigropaleata* (Fig. 6d)
18. Lateral pinnae opposite; terminal pinna less than 10 cm long; rhizome upright, cylindrical or very short-creeping, dorsiventral; stipules present
19. Rhizome upright, cylindrical; terminal pinna more than 4 cm long . . . . . *Danaea leprieurii* (Fig. 4c)
19. Rhizome short-creeping, dorsiventral; terminal pinna less than 4 cm long . . . . . *Danaea nodosa*
17. Base of terminal pinna cuneate to rounded, ending abruptly in a nonalate rachis; pinna apex serrate or with hair-like protrusions
20. Rhizome compact; petiole bases swollen and straight; stipules present; lateral pinnae usually opposite with a dark and slightly swollen node in the rachis . . . . . *Danaea ulei* (Fig. 5b,c)
20. Rhizome long-creeping; petiole bases slender and curved; stipules absent; lateral pinnae subopposite, nodes absent
21. Pinna apex entire, with hair-like protrusions; leaf margin conspicuously pale and cartilaginous; pinnae more than 3 cm wide . . . . . *Salpichlaena volubilis* (Fig. 5e)
21. Pinna apex serrate; leaf margin concolorous with the lamina, not or hardly cartilaginous; pinnae usually less than 3 cm wide . . . . . *Salpichlaena hookeriana* (Fig. 8a)
16. Leaves with more than three pinnae
22. Pinnae coarsely serrate to lobed, pinnatifid; leaves usually shorter than 15 cm
23. Terminal pinna smaller than the lateral ones; pinna margins lobed with the basal acroscopic pinnule deeply incised and distinctly longer than the other pinnules . . . . . *Metaxya rostrata* (Fig. 7a)
23. Terminal pinna larger than the lateral ones; pinna margins irregularly serrate, basal acroscopic pinnule not distinctly different . . . . . *Saccoloma elegans* (Fig. 7c)
22. Pinnae entire or serrate, not lobed; leaves usually longer than 15 cm
24. Petiole base swollen; stipules present; rachis with dark and slightly swollen nodes at the base of the opposite lateral pinnae
25. Rhizome upright, cylindrical; pinna apex entire or shallowly crenate; leaves less than 70 cm long; nodes usually present in the petiole . . . . . *Danaea leprieurii* (Fig. 4d)
25. Rhizome creeping, dorsiventral; pinna apex serrate or with hair-like protrusions; leaves may exceed 2 m in length; petiole lacking nodes
26. Terminal pinna less than 22 cm long, smaller than lateral ones unless leaves shorter than about 30 cm; pinna apex cuspidate to caudate and serrate . . . . . *Danaea nodosa* (Fig. 7a,b)
26. Terminal pinna more than 22 cm long, equal or larger than the lateral pinnae; pinna apex acuminate and entire with hair-like protrusions . . . . . *Danaea ulei* (Fig. 5b)
24. Petiole base slender; stipules and nodes absent; lateral pinnae alternate or subopposite

27. Rhizome dorsiventral; pinna apex entire . . . . . *Lomariopsis nigropaleata* (Fig. 6d)
27. Rhizome cylindrical; pinna apex serrate or with hair-like protrusions
    28. Pinna margin distinctly pale and cartilaginous; pinna apex with hair-like protrusions . . . . . *Salpichlaena volubilis* (Fig. 5e)
    28. Pinna margin not or hardly cartilaginous; pinna apex serrate
        29. Rhizome densely covered with yellow to brown trichomes; pinna apex coarsely serrate to lobed . . . . . *Metaxya rostrata* (Fig. 7b)
        29. Rhizome glabrous or with linear-lanceolate dark brown scales; pinna apex evenly serrate
            30. Pinna margin serrate; whole petiole red, rachis red or yellow, midrib yellow . . . . . *Saccoloma elegans* (Fig. 7d)
            30. Pinna margin entire; only base of petiole reddish brown, otherwise petiole and midrib pale . . . . . *Salpichlaena hookeriana* (Fig. 8b)

Description of the Species

Each of the species descriptions below starts with a list of those characteristics that remain constant in plants of different sizes. Then follows an account of all morphological changes that have been observed to take place during juvenile development. For full descriptions of the mature stages, see Tryon and Stolze (1989a, 1989b, 1991, 1992, 1993). For each species, an analysis is presented of one or more similar species with which the species in question might be confused, with the plant parts that should be examined for the most important diagnostic characteristics given in parenthesis.

Asplenium serratum L. (Fig. 1a,b)

Description.—*Asplenium serratum* can be recognized by the combination of a rosette-like growth form, simple leaves and parallel, straight, almost always bifurcate veins that spread at 30–75° from the midrib. The rhizome and petiole bear dark brown, clathrate, linear scales up to 3 mm long, and close to the midrib on the abaxial side of the lamina there are scales provided with long marginal cilia. The midrib is flat or rounded, most protruding at the base of the abaxial side.

In the smallest leaves (less than 5 cm long) the leaf base extends to the base of the petiole and the margin may be irregularly lobed. The lamina of larger leaves is entire and (linear-)elliptic, usually with an acuminate apex, sometimes acute or cuspidate. The leaf base is either long-attenuate and gradually tapering, or inequilateral with a short (to 2 cm) petiole. The margins are entire or crenulate to serrate.

The dried leaves are green with a yellowish, greyish or dark brown tint, and thin to moderately thick.

Taxonomic Problems.—Tryon and Stolze (1993) maintain *A. serratum* separate from *A. angustum*, *A. pseudoangustum* and *A. stuebelianum* on the basis of the width of the leaf, the length of the petiole, and the angle of the veins. However, there is so much gradual variation in our material that we have not attempted to separate these species here.

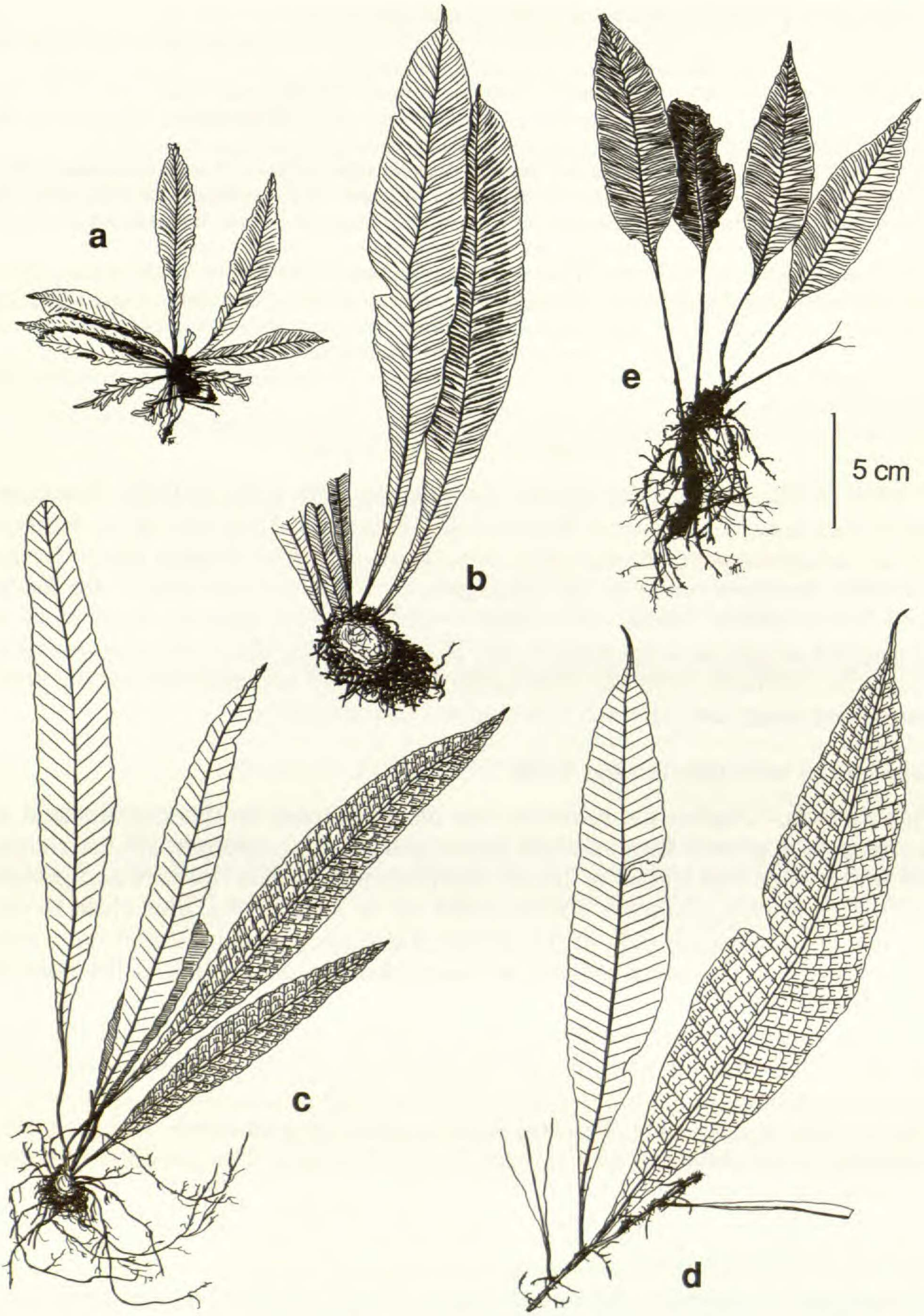

FIG. 1. **a–b**. *Asplenium serratum*. **a**. Juvenile (*Tuomisto et al. 2486*). **b**. Mature (*Tuomisto et al. 2350*). **c**. *Campyloneurum phyllitidis* (*Tuomisto et al. 2715*). **d**. *Campyloneurum repens* (*Tuomisto et al. 5280*; the distance between veinlets is exaggerated). **e**. *Elaphoglossum discolor* (*Tuomisto et al. 2453*).

POTENTIAL MISDETERMINATION.—*Campyloneurum repens* (venation), *C. phyllitidis* (venation), *Cyclodium meniscioides* (venation), *Lomariopsis nigropaleata* (rhizome, vein angle).

Bolbitis nicotianifolia (Sw.) Alston (Fig. 2a–d)

DESCRIPTION.—*Bolbitis nicotianifolia* has a characteristic anastomosing venation: the parallel veins are connected by curved veinlets between which smaller veinlets form numerous cell-like areoles with free included veinlets pointing to various directions. The margin of the lamina is entire to somewhat crenate. The petiole and rachis are usually rounded abaxially and grooved adaxially.

According to Hennipman (1977), the first leaves (about 2 cm long) are lobed, and with increasing size the lobing becomes shallower. The smallest leaves in our material are 6 cm long and simple, and they have long acuminate apices and entire margins. The epiphytic juveniles have elliptic leaves, while in the terrestrial ones the leaves are more lanceolate. Larger juveniles become pinnate with a nonalate rachis. The pinnae are elliptic to oblong or even oblanceolate in large leaves, with acuminate to cuspidate apex. The base of the terminal pinna is attenuate while the lateral ones can also be cuneate to obtuse. The upper lateral pinnae are often narrowly decurrent, but the lower ones are short-stalked. The distance between veins is 3 mm in small leaves, and increases to 6–13 mm in large leaves.

Terrestrial individuals have a long-creeping, usually less than 4 mm thick rhizome, while the epiphytic ones have a thicker short-creeping rhizome. When terrestrial individuals grow in wet soil, the rhizome becomes exceptionally long-creeping and the scales sparcely scattered. The scales on the rhizome and petiole are linear, dark brown and about 5 mm long in small leaves, 10 mm in large ones.

The dried leaves are thin and greyish green to brownish with the abaxial side lighter in color and more shiny. Sometimes there is a distinct pale zone along the midrib.

POTENTIAL MISDETERMINATION.—Simple leaves: *Campyloneurum phyllitidis* (venation), *C. repens* (venation), *Cyclodium meniscioides* (venation), *Thelypteris macrophylla* (venation). Pinnate leaves: *C. meniscioides* (venation), *T. macrophylla* (venation).

Campyloneurum phyllitidis (L.) C. Presl (Fig. 1c)

DESCRIPTION.—*Campyloneurum phyllitidis* is characterized by the venation pattern: parallel veins spread at 45–70° from the midrib, about 3–6 mm apart, and are connected by curved veinlets about 3 mm apart that give rise to 2–4 excurrent veinlets in each areole. Most of the excurrent veinlets are free but some form secondary areoles. The base of the midrib may be grooved to somewhat protruding. The lamina is linear-elliptic and gradually becomes more

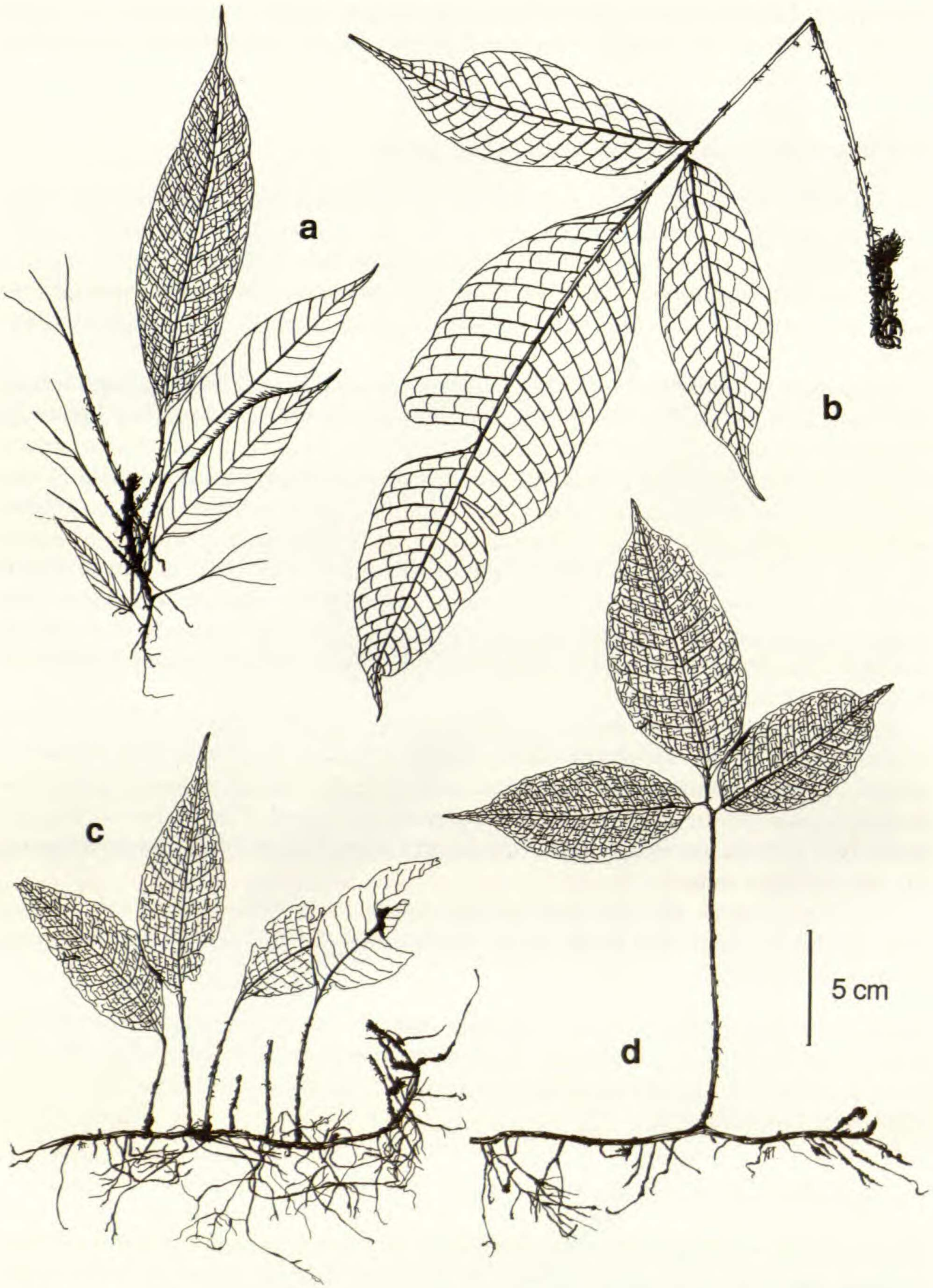

FIG. 2. **a–d**. *Bolbitis nicotianifolia*. **a**. Climbing juvenile with simple leaves (*Tuomisto et al. 3081*). **b**. Climbing juvenile with pinnate leaves (*Tuomisto et al. 5842*; distance between veinlets exaggerated, smallest veinlets not shown). **c**. Terrestrial juvenile with simple leaves (*Tuomisto et al. 5734*). **d**. Terrestrial juvenile with pinnate leaves (*Tuomisto et al. 5758*).

parallel-sided in larger leaves. The leaf margin is entire and the apex acute to acuminate. The rhizome is short-creeping with the distance between adjacent leaf bases being less than the diameter of the rhizome, which may exceed 5 mm in large individuals. The apex of the rhizome is covered by brown lanceolate scales 2–3 mm long.

The color of the dried leaves is greyish to yellowish green with a bluish shade.

TAXONOMIC PROBLEMS.—This species may eventually turn out to be another species close to *C. phyllitidis*; we use the name here in a wide sense.

POTENTIAL MISDETERMINATION.—*Asplenium serratum* (venation), *Bolbitis nicotianifolia* (venation), *Campyloneurum repens* (venation, rhizome), *Cyclodium meniscioides* (venation), *Lomariopsis nigropaleata* (venation).

Campyloneurum repens (Aublet) C. Presl (Fig. 1d)

DESCRIPTION.—*Campyloneurum repens* can be recognized by the regular venation of parallel veins usually 5-7(–10) mm apart, spreading at about 70–90° from the midrib and connected by rather straight veinlets that are 2-3(–4) mm apart and give rise to two excurrent free veinlets in each areole. The midrib is abaxially protruding as a distinct, narrow wing; adaxially it is usually flat to slightly grooved. The lamina is narrow-elliptic and becomes more parallel-sided in large leaves. The leaf margin is entire to slightly sinuate or crenate, and the apex is acuminate. The rhizome is long-creeping with the distance between adjacent leaf bases several times longer than the diameter of the rhizome, which is usually less than 3 mm. The rhizome is covered by brown narrowly lanceolate scales about 2–3 mm long.

The color of the dried leaves is greenish brown and the leaves are thin.

TAXONOMIC PROBLEMS.—This species may eventually turn out to be another species close to *C. repens*; we use the name here in a wide sense.

POTENTIAL MISDETERMINATION.—*Bolbitis nicotianifolia* (venation), *Campyloneurum phyllitidis* (venation, rhizome), *Cyclodium meniscioides* (venation).

Cyclodium meniscioides (Willd.) C. Presl (Fig. 3a–c)

DESCRIPTION.—*Cyclodium meniscioides* can be recognized by the herring-bone venation pattern formed by veinlets that converge in a sharp angle and often unite to give rise to a free excurrent veinlet. The distance between veins is variable but usually in the range 3–8 mm. The leaf apex is acuminate. The petiole, rachis and midrib are prominent or rounded abaxially and grooved adaxially.

The smallest leaves (shorter than about 10 cm) are simple and linear-lanceolate in shape, gradually reduced to a long-attenuate base. The margins are lobed to sinuate. Some veinlets are anastomosing, but the herring-bone pattern and the difference between veins and veinlets are not yet very clear. In larger

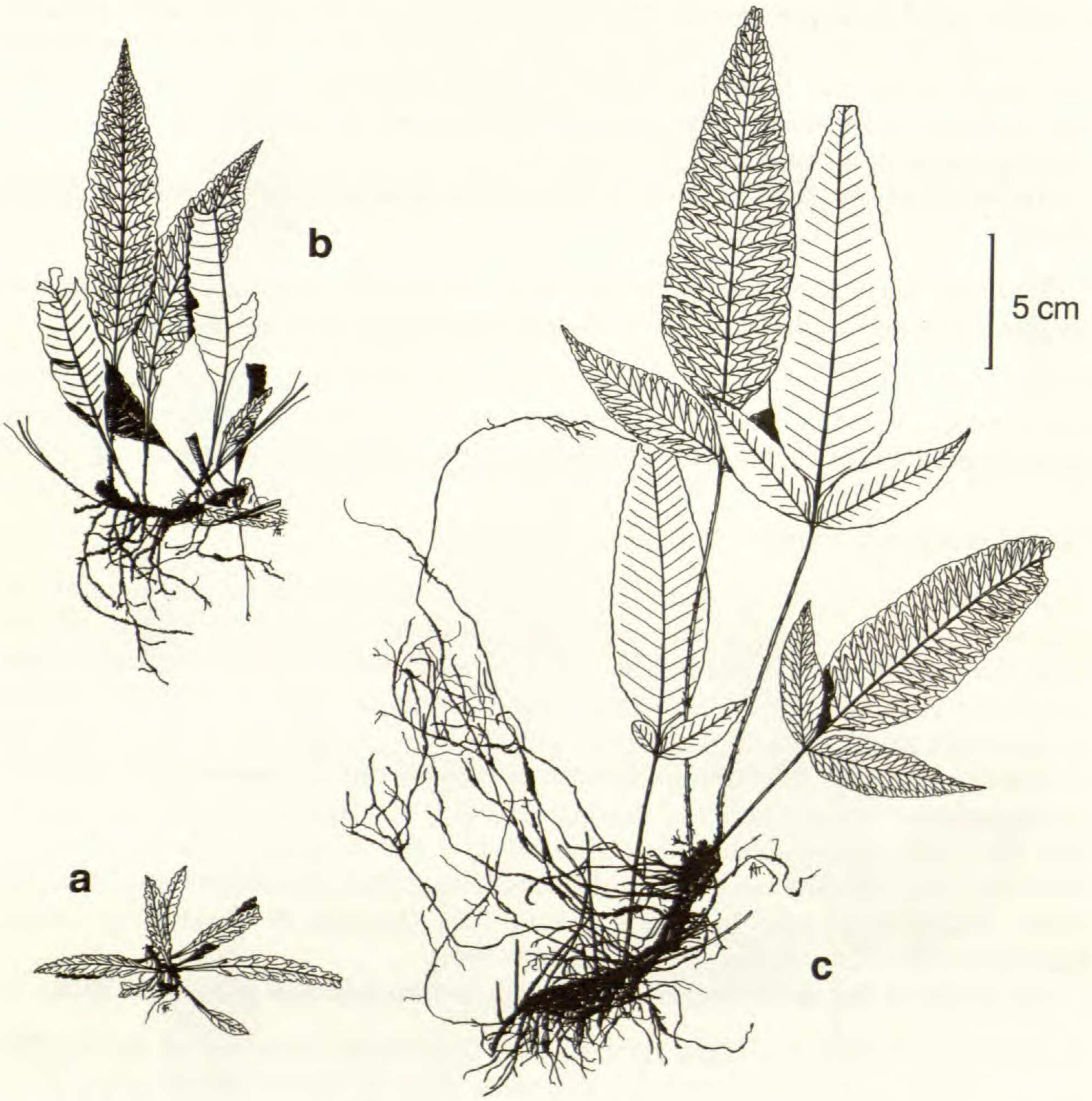

FIG. 3. **a–c**. *Cyclodium meniscioides*. **a**. Juvenile with incompletely developed venation (*Tuomisto et al. 1141*). **b**. Juvenile with developing petiole (*Tuomisto et al. 2294*). **c**. Juvenile with pinnate leaves (*Tuomisto et al. 1150*).

leaves the attenuate base becomes shorter and a distinct petiole develops. Simple leaves up to 36 cm long have been seen, while the smallest pinnate leaves are 20 cm long. The first pinnate leaves have one or two small lateral pinnae, and when the leaves become larger both the number and relative size of the lateral pinnae increase. The lateral pinnae are usually alternate. The base of the terminal pinna is attenuate and that of the lateral pinnae rounded or cuneate and often asymmetric. The rachis is nonalate. The rhizome and petiole base bear reddish brown linear scales, 3 mm long in small leaves and up to 15 mm long in big ones. The rhizome is creeping and may become 2 cm thick in large individuals.

Cyclodium meniscioides can be either terrestrial or climbing on the lower parts of tree trunks. When terrestrial individuals grow on wet soil, the rhizome becomes exceptionally long-creeping and the scales sparsely scattered.

The dried leaves are greyish brown with the adaxial side distinctly darker and more shiny, abaxial side more yellowish. The leaves are moderately thick.

POTENTIAL MISDETERMINATION.—Simple leaves without petiole: *Asplenium serratum* (venation), *Lomariopsis nigropaleata* (venation). Simple leaves with petiole: *Bolbitis nicotianifolia* (venation), *Campyloneurum repens* (venation), *C. phyllitidis* (venation), *Thelypteris macrophylla* (venation). Pinnate leaves: *B. nicotianifolia* (venation), *T. macrophylla* (venation).

Danaea leprieurii Kunze (Fig. 4c,d)

DESCRIPTION.—*Danaea leprieurii* can be recognized by the erect symmetrical rhizome, swollen petiole bases, presence of stipules, parallel veins that are usually bifurcate at the base, and entire to shallowly crenate or undulating leaf margin and apex. The midrib is slightly protruding abaxially. Usually, although not always, the petiole has one or a few nodes. The scales are small and peltate.

The lamina of the simple leaf is ovate with an acute apex, although in very small leaves (less than 2 cm long) the apex is obtuse. The leaves become pinnate when they are still less than 15 cm long. In the first stage the terminal pinna retains the ovate shape of the simple leaf, and there is one pair of small lateral pinnae. Later both the number and size of the lateral pinnae increase and the terminal pinna becomes longer in shape until the pinnae are almost uniform. Then the pinnae are up to 10(–16) cm long and 3 cm wide, lanceolate with an acuminate to caudate apex. The terminal pinna tends to be slightly broader than the lateral ones, and it has a cuneate base, while the lateral pinnae have inaequilateral bases. The lateral pinnae are opposite, and the alate rachis has a node at the pinna base. The almost straight veins spread at 80–90° from the midrib and their density is usually 8–12 per cm. The erect stem consists of the rhizome and the persistent leaf bases and stipules, and its diameter is usually less than 1 cm, although it may be as much as 2 cm in very robust individuals.

The dried leaves are dark green to blackish brown and thin.

TAXONOMIC PROBLEMS.—This species keys to *D. elliptica* when identified according to Tryon and Stolze (1989a); their treatment does not include the name *D. leprieurii*. Tryon and Stolze expressed doubts concerning the distinctness of *D. elliptica* and *D. nodosa*, and they indeed may be correct in that these two names are synonymous. Our specimens do not match the type of *D. elliptica*, but as they do match a photograph of the type of *D. leprieurii*, we adopt the latter name here. Among our specimens, there seem to be two forms; the more robust one is often more than 40 cm tall, has pinnae longer than 10 cm, and has a rhizome more than 1 cm thick, while the smaller form is more common and matches the type better. As the material is not sufficient to decide whether two taxa are involved, the forms are treated together here. Even so,

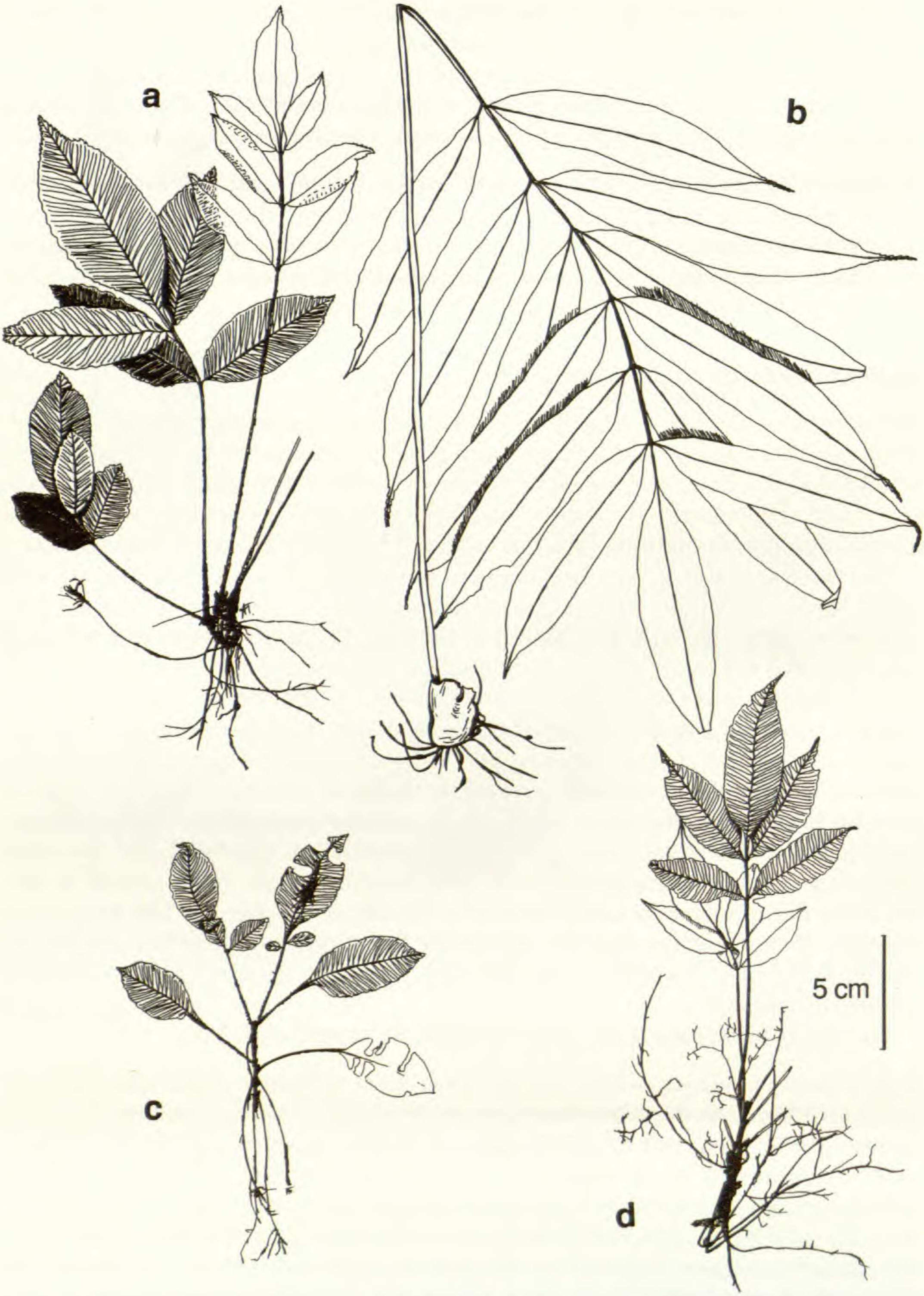

FIG. 4. **a–b**. *Danaea nodosa*. **a**. Juvenile with terminal pinna larger than the lateral ones (*Tuomisto et al. 3051*). **b**. Juvenile with terminal pinna smaller than the lateral ones (*Tuomisto et al. 3226*). **c–d**. *Danaea leprieurii*. **c**. Juvenile with simple leaves (*Tuomisto et al. 2003*). **d**. Juvenile with leaves having five pinnae (*Tuomisto et al. 2028*).

TABLE 1. The diagnostic characteristics of *Danaea leprieurii*, *D. nodosa* and *D. ulei*.

	D. leprieurii	*D. nodosa*	*D. ulei*
Rhizome	erect, symmetrical	horizontal, dorsiventral	horizontal, dorsiventral
Shape of simple leaves	lanceolate to ovate	orbiculate	linear-lanceolate to elliptic
Shape of apex in simple leaves	obtuse to acute	obtuse	acuminate
Maximum length of simple leaves	13 cm	4 cm	46 cm
Maximum length of lamina in simple leaves	9 cm	2 cm	21 cm
Maximum width of simple leaves	2.7 cm	1.5 cm	5.6 cm
Length of leaves with three pinnae	6–15 cm	3–6 cm	49–75 cm
Length of leaves with more than three pinnae	13–68 cm	5 cm–over 2 m	40 cm–over 2 m
Shape of pinnae	ovate to lanceolate	elliptic to ovate in plants less than 30 cm tall; in larger plants (linear-) oblanceolate to obovate	linear-elliptic to oblanceolate
Shape of pinna apex	acuminate to caudate	acute in small leaves, acuminate to cuspidate in large leaves	acuminate
Margin of pinna apex	entire or shallowly crenate	serrate	entire or with hair-like dentations
Length of terminal pinna	4–14 cm	2–21 cm	22–37 cm
Length of lateral pinnae	1–16 cm	1–25 cm	14–39 cm
Width of pinnae	0.5–3.6 cm	0.5–4.9 cm	3.5–7.8 cm
Relative size of pinnae in small plants	terminal pinna several times larger than lateral ones	terminal pinna several times larger than lateral ones	terminal pinna less than twice the size of lateral ones
Relative size of pinnae in large plants	lateral pinnae in the middle of rachis largest	basal pinnae largest, up to twice the length of terminal one	pinnae almost equal in size
Rachis	alate	usually alate	nonalate
Number of veins per cm	8–16	10–15 in small leaves, 16–22 in large leaves	8–13 in small leaves, 10–19 in large leaves
Iridescence in juveniles	absent	present	present

D. leprieurii is clearly distinct from the other species of *Danaea* on the basis of several characteristics (Table 1).

POTENTIAL MISDETERMINATION.—Simple leaves: *Danaea nodosa* (rhizome, leaf apex, lamina size), *D. ulei* (rhizome, leaf apex, lamina size), *Elaphoglossum discolor* (rhizome, color), *Salpichlaena hookeriana* (rhizome, leaf apex), *S. volubilis* (rhizome, leaf margin). Pinnate leaves: *D. nodosa* (rhizome, leaf apex).

Danaea nodosa (L.) J. E. Sm. (Fig. 4a,b)

DESCRIPTION.—*Danaea nodosa* has swollen petiole bases with stipules, petioles that lack nodes, serrate pinna apices, and parallel veins that are usually bifurcate at the base. The scales are small and peltate.

The first leaves are simple and have an orbicular lamina up to 1.5 cm in diameter. As soon as lateral pinnae are produced, the terminal pinna becomes ovate with an acute apex. The first pair of small lateral pinnae is produced very early, and by the length of about 5 cm, the leaves already have two pairs of lateral pinnae. In small plants (less than about 30 cm) the terminal pinna is larger than the lateral pinnae. At this stage, all pinnae are ovate with an acuminate apex, but when they get larger they become obovate to linear-oblanceolate with a cuspidate to caudate apex. The width of the larger pinnae is 3–6 cm. The terminal pinna is cuneate at the base, while the lateral pinnae are inequilateral. The rachis is alate, most distinctly so in the upper part of the internodes, and the nodes between the opposite lateral pinnae are slightly swollen. The rachis and midrib are shallowly grooved adaxially; abaxially the rachis is rounded and the midrib sharply protruding. The leaf margin is often undulating. The veins spread at 80–90° from the midrib, and their density generally increases with leaf size: in small leaves there may be as few as 10 veins per cm, while in large leaves there are at least 16 per cm and often more than 20 per cm. The rhizome is dorsiventral, and although it may be erect in small plants, it becomes horizontal, short-creeping and bulky by the time the leaves attain the length of about 40 cm. The petiole bases are distinctly swollen and a few times as thick as the petiole; in large plants the rhizome may therefore seem more than 2 cm thick.

The dried plants are shiny green to dark green with moderately thin leaves. Fresh leaves are succulent, and the juveniles are iridescent.

TAXONOMIC PROBLEMS.—Tryon and Stolze (1989a) listed for Peru only one species of *Danaea* that is robust and lacks nodes in the petiole, namely *D. nodosa*, but also *D. ulei* has these characteristics although it is clearly distinct in several other respects (Table 1). It may furthermore turn out that the name *D. nodosa* is not applicable to our material after all. The type of this species is a drawing from the Caribbean that shows entire pinna apices, as do many *Danaea* collections from that region, but unlike Amazonian collections which have serrate apices. For further discussion, see under *D. leprieurii* and *D. ulei*.

POTENTIAL MISDETERMINATION.—Simple leaves: *Danaea leprieurii* (rhizome, leaf shape and size), *D. ulei* (leaf shape and size), *Elaphoglossum discolor* (rhizome, leaf shape and size). Pinnate leaves: *Danaea leprieurii* (rhizome, leaf apex), *D. ulei* (pinna shape and size), *Lomariopsis nigropaleata* (rhizome, pinna position), *Salpichlaena volubilis* (rhizome, leaf margin).

Danaea ulei Christ (Fig. 5a–c)

DESCRIPTION.—*Danaea ulei* has stipules and distinctly swollen petiole bases, and a petiole that lacks nodes. The leaf margin is pale and brownish but not

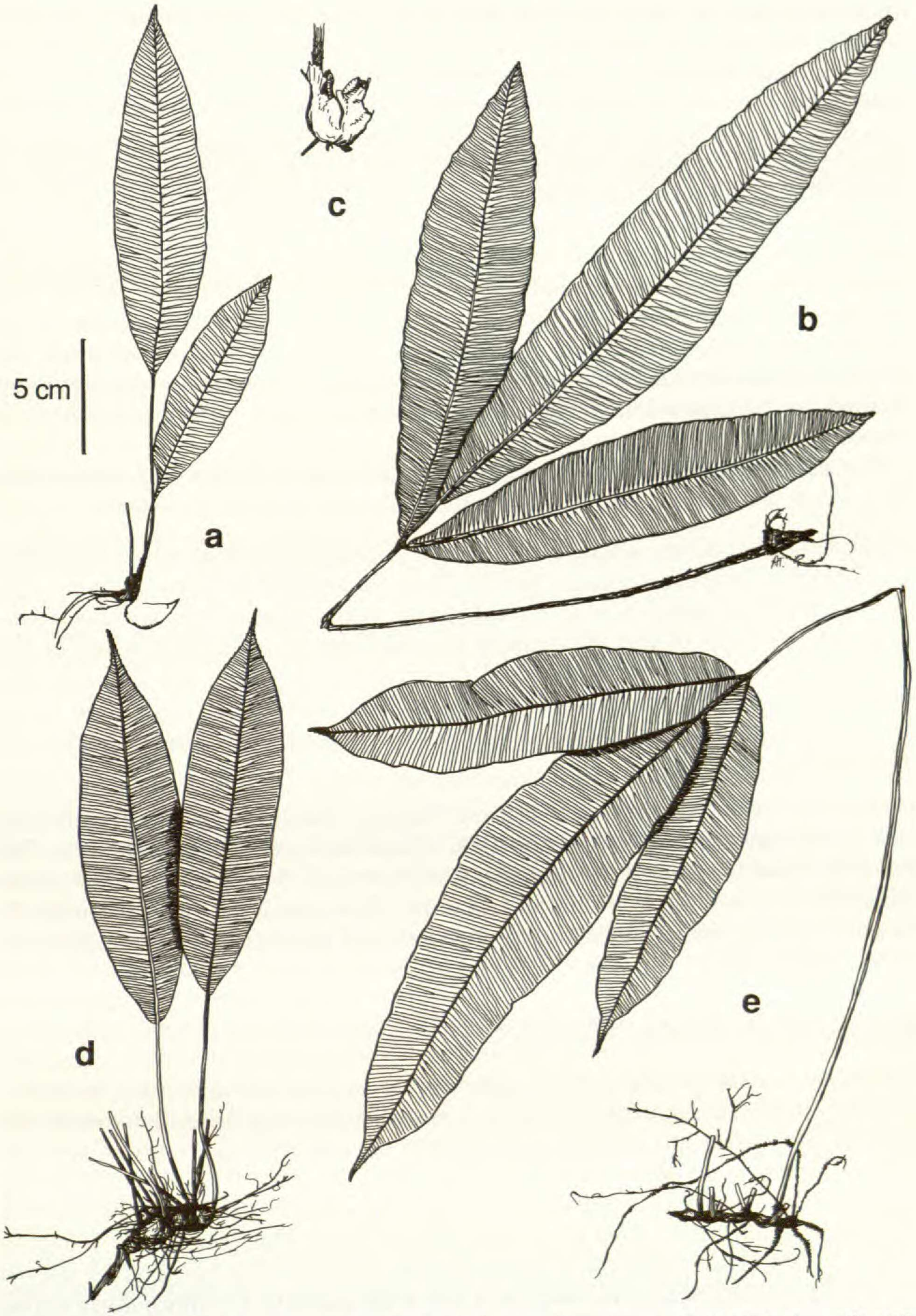

FIG. 5. **a–c**. *Danaea ulei*. **a**. Juvenile with simple leaves (*Tuomisto et al. 4136*). **b**. Juvenile with pinnate leaves having three pinnae (*Tuomisto et al. 4143*). **c**. Part of rhizome showing stipules and the swollen petiole base (*Tuomisto et al. 5256*). **d–e**. *Salpichlaena volubilis*. **d**. Juvenile with simple leaves (*Poulsen 79620*). **e**. Juvenile with pinnate leaves having three pinnae (*Poulsen 79270*).

thickened, and the apex has hair-like protrusions that emerge from the pale margin. The veins are parallel and bifurcating. The scales are small and peltate.

The simple leaves are linear-lanceolate, with an acute apex and a cuneate base. Simple leaves up to 45 cm long and 6 cm wide have been encountered. The first pinnate leaves up to the length of about 70 cm have only one pair of lateral pinnae, the larger ones have more. The pinnae are linear-lanceolate or linear-oblanceolate and cuneate at the base, and the lateral pinnae are shortly stalked. The width of the pinnae is 4–7 cm. The pinnae are opposite, rarely subopposite, and the rachis is nonalate and with slightly swollen nodes at the points where pinnae are attached. Density of veins is about 12–16 per cm. The rhizome is dorsiventral, and although it may be erect in small plants, it becomes horizontal, short-creeping and bulky by the time the leaves attain the length of about 40 cm. The petiole bases are distinctly swollen and a few times as thick as the petiole; in large plants the rhizome may therefore seem more than 2 cm thick.

The dried plants are shiny green to dark greeninsh brown and moderately thin. Fresh leaves are succulent, and the juveniles may be iridescent.

TAXONOMIC PROBLEMS.—This species keys to *Danaea nodosa* when identified according to Tryon and Stolze (1989a). They do not mention the name *D. ulei*, but our material matches well a photograph of the type of this species. However, on the basis of the photograph it could not be confirmed whether the rhizome of *D. ulei* is horizontal and dorsiventral; if this is not the case, the name may not apply to our material after all. For further discussion, see under *D. leprieurii* and *D. nodosa*. The differences among these three species are summarized in Table 1.

POTENTIAL MISDETERMINATION.—Simple leaves: *Danaea leprieurii* (rhizome, leaf apex, lamina size), *D. nodosa* (leaf shape and size), *Elaphoglossum discolor* (rhizome), *Lomariopsis nigropaleata* (rhizome), *Salpichlaena hookeriana* (rhizome, leaf apex), *S. volubilis* (rhizome, leaf margin). Pinnate leaves: *D. nodosa* (pinna shape and size), *L. nigropaleata* (rhizome), *S. volubilis* (rhizome, leaf margin).

Elaphoglossum discolor (Kuhn) C. Chr. (Fig. 1e)

DESCRIPTION.—*Elaphoglossum discolor* has an entire leaf apex and an entire margin, in which a narrow border is colored differently from the rest of the lamina. The veins are parallel and slightly curved with the convex side towards the leaf apex. More than half of the veins are forked, occasionally twice so, and their density is usually 6–8 per cm. The midrib is pronounced on both leaf surfaces, usually more so on the abaxial side. The rhizome is creeping and 1–2 mm thick, although it seems thicker because it is covered by brown (linear-)lanceolate scales that may be 5 mm long (usually 2–3 mm); these scales are also found on the petiole. Both surfaces of the lamina bear small scales that have long teeth.

The smallest leaves (less than 5 cm long) are elliptic with an acute apex and

a broad long-attenuate base. Larger leaves are elliptic or lanceolate with an acuminate apex and attenuate, sometimes cuneate base. The petiole is about ¼ to ½ the length of the leaf and sometimes alate near the lamina.
The leaves are grey to brown and moderately thick.

POTENTIAL MISDETERMINATION.—*Danaea leprieurii* (rhizome, color), *D. nodosa* (rhizome, leaf shape and size), *D. ulei* (rhizome), *Lomariopsis nigropaleata* (venation), *Salpichlaena hookeriana* (leaf apex), *S. volubilis* (leaf margin).

Lomariopsis nigropaleata Holttum (Fig. 6a–d)

DESCRIPTION.—*Lomariopsis nigropaleata* has parallel veins that spread at 80–90° from the midrib. The veins are slightly curved with the convex side towards the leaf apex, and less than half of them are forked. The density of veins is 8–11 per cm. The midrib is pronounced on both sides of the leaf, usually more so abaxially. The rhizome is long-creeping and dorsiventrally flattened, with a characteristically irregular outline shaped by the vascular bundles that lead to the leaves. In very large individuals the rhizome may be 2 cm wide.

The smallest leaves have a lobed margin, which becomes entire to slightly crenulate when the leaves reach the length of about 5 cm. The lamina base is long-attenuate and the apex is first acute, later acuminate to cuspidate. The rhizome is at first covered with spreading, ciliate, brown scales, in larger individuals the scales become black, broadly lanceolate to ovate and appressed, 2–3 mm long. Leaves longer than 20 cm often have a distinct petiole, the length of which is usually less than ½ the length of the leaf. Simple leaves up to 40 cm long have been encountered, while the smallest pinnate leaves are 25 cm long. In the first pinnate leaves the terminal pinna is much larger than the lateral ones, but as the number of lateral pinnae increases the terminal pinna becomes smaller. Rarely, a plant may produce a simple leaf still after it has produced the first leaf with one pair of lateral pinnae. The lateral pinnae are usually alternate with a cuneate to inequilateral base while the base of the terminal pinna is attenuate. The rachis and upper part of petiole are narrowly alate. The pinnae are broadly linear to lanceolate and have entire margins and acuminate to cuspidate apices.

The dried leaves are dark green to dark brown, with the adaxial side usually distinctly darker than the abaxial side. The leaves are thin to moderately thick.

Lomariopsis nigropaleata can grow terrestrially, but usually it is found climbing on tree trunks.

TAXONOMIC PROBLEMS.—*Lomariopsis nigropaleata* is closely related to *L. erythrodes* and *L. japurensis*. It can be distinguished from these on the basis of the rhizome scales and pinna form (Tryon and Stolze, 1991) apparently already at the stage of simple leaf with petiole. However, we have so little juvenile material available of *L. japurensis* and *L. erythrodes* that they are excluded here.

POTENTIAL MISDETERMINATION.—Simple leaves without petiole: *Asplenium serratum* (venation, rhizome), *Campyloneurum phyllitidis* (venation), *C. repens*

FIG. 6. **a–d**. *Lomariopsis nigropaleata*. **a**. Juvenile with simple leaves and lobed margins (*Tuomisto et al. 2423*). **b**. Juvenile with simple leaves without petiole (*Tuomisto et al. 2740*). **c**. Juvenile with simple leaves developing petiole (*Poulsen 79860*). **d**. Juvenile with pinnate leaves (*Tuomisto et al. 2429*).

(venation), *Cyclodium meniscioides* (venation). Simple leaves with petiole: *Danaea ulei* (rhizome), *Elaphoglossum discolor* (venation), *Salpichlaena hookeriana* (rhizome, leaf apex), *S. volubilis* (rhizome, leaf margin). Pinnate leaves: *D. nodosa* (rhizome, pinna position), *D. ulei* (rhizome, pinna position), *S. hookeriana* (rhizome, leaf apex), *S. volubilis* (rhizome, leaf margin).

Metaxya rostrata (Kunth) C. Presl (Fig. 7a,b)

DESCRIPTION.—*Metaxya rostrata* has a short-creeping rhizome with a diameter up to 1 cm, densely covered with yellow to orange or brown trichomes about 5 mm in length. The veins are parallel and usually bifurcating at the base; occasionally two veins fuse closer to the margin. The veins are slightly curved with the concave side towards the leaf apex. Each dentation of the leaf margin is served by one or more veins.

The smallest leaves (less than about 15 cm long) are pinnate with deeply lobed, almost pinnatifid and coarsely serrate margins. The basal acroscopic lobe or pinnule is deeply incised and protruding. The pinnae become smaller towards the pinnatifid leaf apex. When the leaves grow larger, the pinnae gradually become linear-lanceolate, entire and with cuspidate apices, and eventually only the apex of each pinna remains deeply serrate to lobed. In leaves with entire pinnae, the veins spread at 60–80° from the midrib; in small leaves their density is 15–20 per cm, in large ones it decreases to 8–16 per cm. In small leaves all pinnae are decurrent and the rachis is narrowly alate. In larger leaves the wing becomes progressively less marked and ultimately disappears, and the lower pinnae become stalked with a cuneate base.

The dried leaves are brown and moderately thick.

POTENTIAL MISDETERMINATION.—Leaves with pinnatifid pinnae: *Saccoloma elegans* (pinna shape, color). Leaves with entire pinnae: *S. elegans* (pinna margin, color), *Salpichlaena hookeriana* (rhizome, color).

Saccoloma elegans Kaulf. (Fig. 7c,d)

DESCRIPTION.—The leaves of *Saccoloma elegans* are pinnate with parallel and sometimes bifurcating veins; each dentation of the pinna margin is served by one vein. The veins spread from the midrib at an angle of 70–80°, and they are almost straight until they bend towards the leaf apex at the pinna margin. The density of veins is 6–9 per cm. The rhizome is erect and compact, up to 1 cm thick, with brown linear-lanceolate scales up to 6 mm long. Lower lateral pinnae are shortly stalked and most have an inequilateral base, while the upper pinnae are decurrent.

In the smallest leaves (less than about 15 cm long) the pinna margins are coarsely and irregularly serrate to lobed. The terminal pinna is larger than the lateral pinnae, and sometimes connected by an alate rachis to the upper lateral pinnae. The pinnae are more or less lanceolate in shape and the terminal pinna has an acuminate apex. In larger leaves the pinnae become linear with caudate apices, attenuate bases and regularly serrate margins. The rachis is then non-

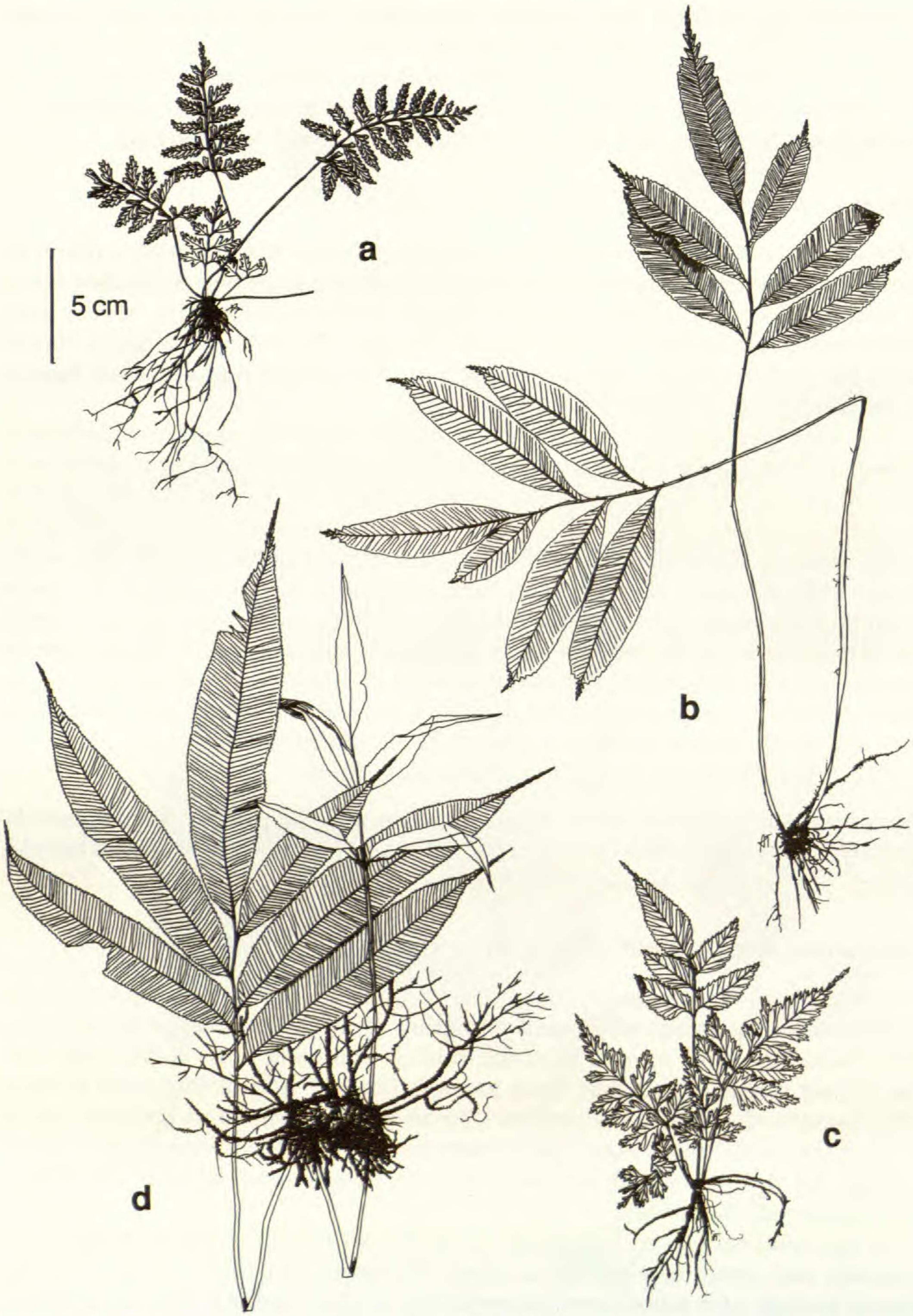

FIG. 7. **a–b**. *Metaxya rostrata*. **a**. Juvenile with lobed pinnae (*Tuomisto et al. 2457*). **b**. Juvenile with entire pinnae (*Tuomisto et al. 2818*). **c-d**. *Saccoloma elegans*. **c**. Juvenile with lobed pinnae (*Tuomisto et al. 3056*). **d**. Juvenile with entire pinnae (*Tuomisto et al. 2684*).

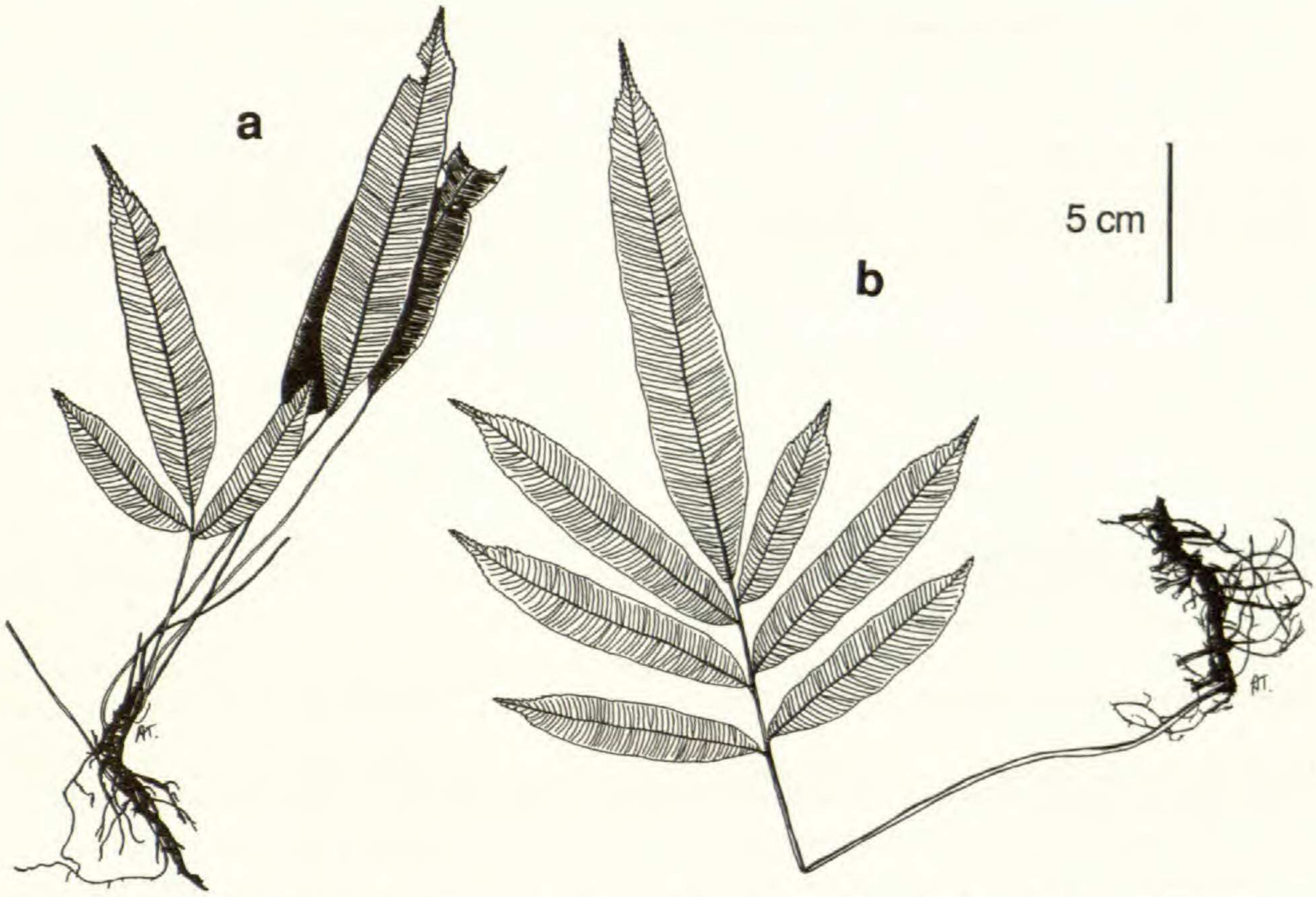

FIG. 8. **a–b**. *Salpichlaena hookeriana*. **a**. Juvenile with simple and pinnate leaves having three pinnae (*Poulsen 80078a*). **b**. Juvenile with more than three pinnae (*Poulsen 80078a*).

alate and sharply grooved on one side, rounded on the other. The midrib is rounded and protruding abaxially, narrower and grooved adaxially.

The dried leaves are green with a shiny reddish petiole and yellow midribs. The lamina is moderately thick.

POTENTIAL MISDETERMINATION.—Leaves with pinnatifid pinnae: *Metaxya rostrata* (pinna shape, color). Leaves with entire pinnae: *M. rostrata* (pinna margin, color), *Salpichlaena hookeriana* (rhizome, pinna margin, color).

Salpichlaena hookeriana (O. Kuntze) Alston (Fig. 8a,b)

DESCRIPTION.—*Salpichlaena hookeriana* is characterized by a creeping rhizome that can become at least 5 mm thick, wiry petiole bases, serrate leaf or pinna apices, concolorous or only narrowly pale leaf margins, and parallel and sometimes bifurcating veins. The veins spread at 70–90° from the midrib, they are slightly curved with the concave side towards the leaf apex, and vein density is 11–19 per cm.

The simple leaves are broadly linear or narrow-elliptic, usually less than 3 cm wide, with an acuminate apex and a cuneate to rounded base. The margin is serrate in small leaves but becomes entire in larger ones, except in the apex. The leaves become pinnate when still less than about 30 cm long, with the lateral pinnae being opposite or alternate and smaller than the terminal one. The pinnae are linear-lanceolate to elliptic, and the rachis between the pinnae

TABLE 2. The diagnostic characteristics of *Salpichlaena hookeriana* and *S. volubilis*.

	S. hookeriana	*S. volubilis*
Margin of leaf or pinna	concolorous, not cartilaginous	pale, cartilaginous
Margin of leaf or pinna apex	serrate	entire or with hair-like dentations
Shape of leaf or pinna apex	acuminate	caudate to cuspidate, sometimes acuminate
Maximum length of simple leaves	31 cm	63 cm
Maximum length of lamina in simple leaves	16 cm	35 cm
Maximum width of simple leaves	3.5 cm	7.0 cm
Length of leaves with three pinnae	20–28 cm	44–71 cm
Length of once pinnate leaves with more than 3 pinnae	25–70 cm	57–135 cm
Length of pinnae in once pinnate leaves	6–18 cm	10–47 cm
Width of pinnae in once pinnate leaves	1.3–3.8 cm	3.2–10 cm
Length of ultimate pinnae in twice pinnate leaves	11–33 cm	11–35 cm
Width of ultimate pinnae in twice pinnate leaves	1.7–5.8 cm	2.5–9.5 cm
Shape of ultimate pinnae	linear-lanceolate to elliptic	elliptic to oblanceolate
Shape of veins	slightly curved with concave side towards leaf apex	straight or slightly curved with convex side towards leaf apex
Number of veins per cm	11–19	10–15
Width of ultimate pinnae in fertile leaves	less than 1 cm	more than 1 cm
Proliferous buds in climbing leaves	usually present	absent

is nonalate. When the leaves reach a sufficient size, they become bipinnate with a several meters long, scrambling petiole; non-climbing leaves longer than 70 cm have not been seen. The ultimate pinnae are broadly linear to elliptic. The climbing leaves may have proliferous buds at the base of the pinnae. When these sprout, they repeat the juvenile development series by first producing simple and then once-pinnate leaves. The midrib is rounded and protruding abaxially, narrower and grooved adaxially; also the rachis is sharply grooved. The dried leaves are adaxially bright to dark green, abaxially grey-green, and moderately thin. The petiole is reddish brown at the base, otherwise pale.

TAXONOMIC PROBLEMS.—Tryon and Stolze (1993) consider *S. hookeriana* as a synonym of *S. volubilis* and note that further study is necessary before another taxon can be recognized with confidence. In western Amazonia, these species are clearly distinct on the basis of several characteristics (Table 2). Outside western Amazonia, there seems to be considerable geographical variation within the genus, and it may eventually turn out that it contains more than two species.

POTENTIAL MISDETERMINATION.—Simple leaves: *Danaea leprieurii* (rhizome, leaf apex, color), *D. ulei* (rhizome, leaf apex), *Elaphoglossum discolor* (leaf apex), *Lomariopsis nigropaleata* (rhizome, leaf apex), *Salpichlaena volubilis* (leaf apex and margin). Pinnate leaves: *D. leprieurii* (rhizome, pinna apex, color), *L. nigropaleata* (rhizome, pinna apex), *Metaxya rostrata* (rhizome, pinna margin, color), *Saccoloma elegans* (rhizome, pinna margin, color), *S. volubilis* (pinna margin and apex, leaf size).

Salpichlaena volubilis (Kaulf.) Hooker (Fig. 5d,e)

DESCRIPTION.—*Salpichlaena volubilis* has a creeping rhizome up to 1 cm thick, wiry petiole bases and rounded or cuneate leaf bases. The leaf or pinna margin is distinctly cartilaginous and lighter in color than the lamina. The leaf or pinna apex is entire but with hair-like protrusions that emerge from the cartilaginous part and do not extend to the green leaf tissue. The parallel and sometimes bifurcating veins are straight or slightly curved with convex side towards the leaf apex. The veins spread at 70–85° from the midrib, and their density is 10–15 per cm.

The shape of the simple leaves is elliptic to broadly linear with an acuminate to caudate apex and a cuneate to rounded base. The midrib is abaxially protruding and adaxially grooved, except at the very apex. Simple leaves may reach a length of more than 60 cm, while pinnate leaves less than 44 cm have not been encountered. In the once pinnate juvenile leaves all pinnae have a cuneate to rounded base, although the lateral ones tend to be more rounded than the terminal one. The lateral pinnae are decurrent to shortly stalked and the rachis is nonalate. When the leaves reach the length of about 1.5 m, they become bipinnate with a long, scrambling petiole and elliptic to oblanceolate ultimate pinnae. The climbing leaves lack proliferous buds. The midrib is rounded and protruding abaxially, narrower and grooved adaxially; also the rachis is sharply grooved.

The dried leaves are adaxially bright to dark green and abaxially grey-green and rather thick, leatherlike. The petiole is reddish brown at the base, otherwise pale.

TAXONOMIC PROBLEMS.—See discussion under *Salpichlaena hookeriana*. The characteristics of both species are summarized in Table 2.

POTENTIAL MISDETERMINATION.—Simple leaves: *Danaea leprieurii* (rhizome, leaf margin, leaf size), *D. ulei* (rhizome, leaf margin), *Elaphoglossum discolor* (rhizome, leaf margin), *Lomariopsis nigropaleata* (rhizome, leaf margin), *Salpichlaena hookeriana* (leaf margin, leaf apex, leaf size). Pinnate leaves: *D. nodosa* (rhizome, leaf margin, leaf size), *D. ulei* (rhizome, leaf margin), *L. nigropaleata* (rhizome, leaf margin), *S. hookeriana* (leaf margin, apex).

Thelypteris macrophylla (Kunze) Morton (Fig. 9a,b)

DESCRIPTION.—*Thelypteris macrophylla* can be recognized by the regular venation: veinlets converge in a blunt angle with each pair giving rise to one free

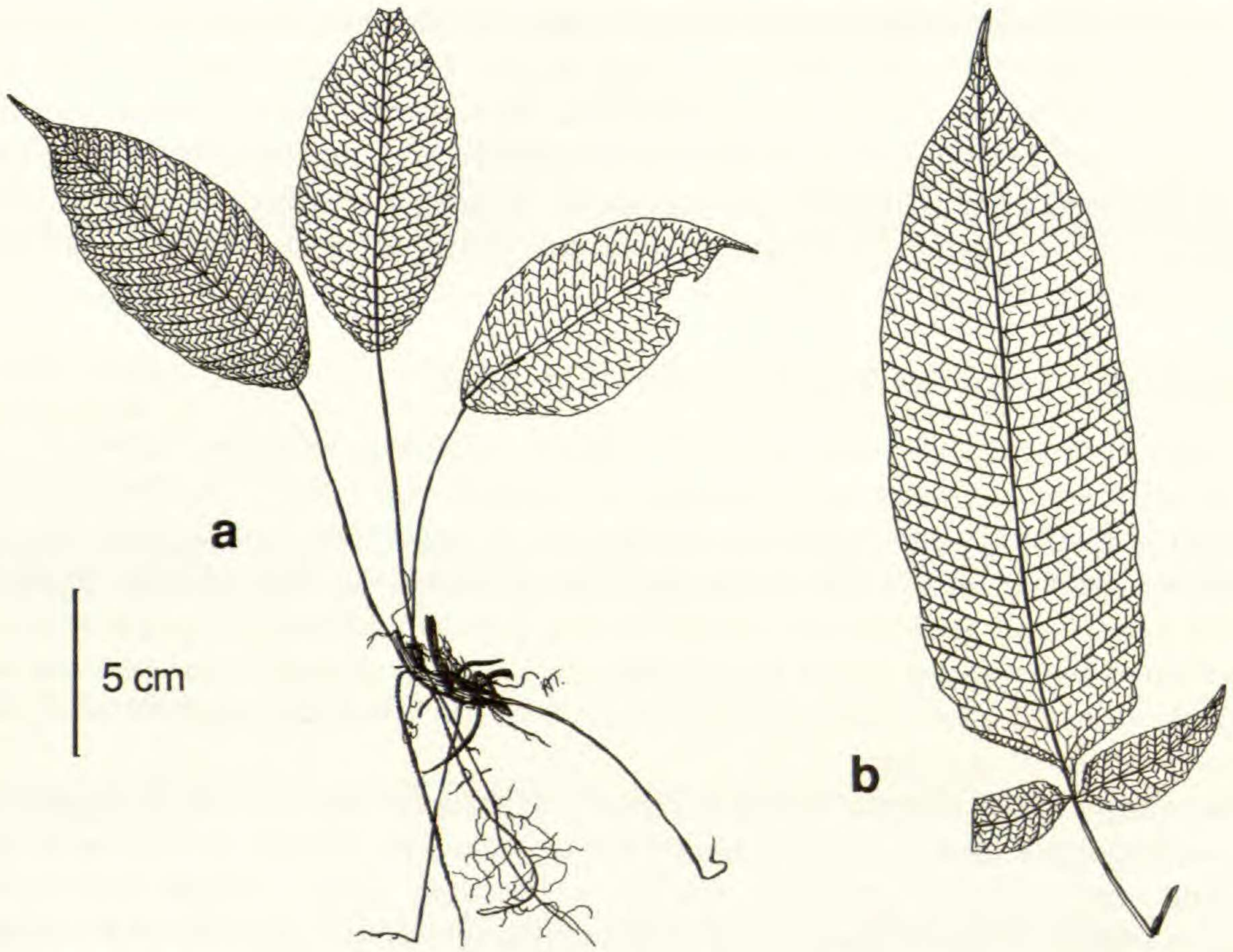

FIG. 9. **a–b**. *Thelypteris macrophylla*. **a**. Juvenile with simple leaves (*Tuomisto et al. 4769*; the distance between veinlets is exaggerated). **b**. Juvenile with pinnate leaves having three pinnae (*Tuomisto et al. 5251*; the distance between veinlets is exaggerated).

excurrent veinlet that points to the margin of the leaf. The distance between the veins is 4–7 mm and between veinlets about 2 mm. The midrib is flat and grooved adaxially, and rounded, sharply protruding abaxially. The leaf margin is entire or shallowly and irregularly sinuate. The rhizome is creeping and up to 1 cm thick in large plants.

The simple leaves are elliptic with acuminate apex and rounded base. The petiole is about ½ the length of the leaf. The first pinnate leaves have one pair of small lateral pinnae, in larger leaves both the size and number of lateral pinnae increase. The shape of the lateral pinnae is usually elliptic but varies from oblanceolate to oblong and lanceolate. The lateral pinnae are usually alternate, sometimes opposite. The base of the terminal pinna is attenuate or cuneate and that of the lateral pinnae is cuneate or rounded, in upper pinnae sometimes decurrent. Lower pinnae are short-stalked.

The dried leaves are brown with the adaxial side darker, and moderately thin.

POTENTIAL MISDETERMINATION.—*Bolbitis nicotianifolia* (venation), *Cyclodium meniscioides* (venation).

Discussion

The fern species that have pinnate leaves with entire, elongate pinnae seem to follow one of three main pathways of juvenile development: 1) The first leaves are simple, and pinnate leaves are produced once the plant has reached a sufficient size. This is a common condition; 2) The juveniles are essentially similar in form to the adults, although they may have fewer pinnae. This is the case at least in *Bolbitis lindigii, Lomagramma guianensis, Lomariopsis fendleri, Trichomanes pinnatum* and probably also in several species of *Thelypteris*. These species were excluded from the present study; 3) The first leaves are pinnate with pinnatifid pinnae, i.e. more complex than the adult stage. This pattern we know only from *Metaxya rostrata* and *Saccoloma elegans*.

Among those species that start with a simple leaf, there are some noteworthy differences. The length attained by the simple leaves before the first pinnate leaves are produced varies from about 5 cm in *Danaea nodosa* to more than 60 cm in *D. ulei* and *Salpichlaena volubilis*. Also the relative size of the pinnae differs. All pinnae are about the same size in *Bolbitis nicotianifolia, D. ulei* and *S. volubilis*. In contrast, *Cyclodium meniscioides, D. leprieurii, D. nodosa, Lomariopsis nigropaleata, Salpichlaena hookeriana* and *Thelypteris macrophylla* first produce pinnate leaves where the lateral pinnae are much smaller than the terminal one. Later the relative and often also the absolute size of the terminal pinna decreases, until it is of the same size or smaller than the lateral pinnae.

Some congeneric species are actually easier to distinguish from each other as juveniles than as adult plants, for example *Danaea ulei* and *D. nodosa*, and *Salpichlaena volubilis* and *S. hookeriana*. In each of these species pairs, the first one produces very large simple leaves, whereas the second becomes pinnate at a much earlier stage. Both in the simple and once pinnate phases, however, *S.volubilis* and *D.ulei* are strikingly similar and can easily be confused, although the adult bipinnate leaves of *Salpichlaena* are entirely unlike anything found in *Danaea*. In the field, these genera can be easily recognized: *Danaea* has succulent and thick leaves and excretes a copious gelatinous substance from the rhizome when cut, whereas the leaves of *Salpichlaena* are relatively thin and the whole plant gives a dry impression. During drying, the leaf texture of *Salpichlaena* hardly changes, while the leaves of *Danaea* become much thinner and the swelling of the nodes is considerably reduced, contributing to the similarity of these species on a herbarium sheet. On the other hand, the characteristic cartilaginous leaf margin of *S. volubilis* is easier to see in dried specimens than in fresh ones.

When samples of *Metaxya rostrata* are preserved with alcohol prior to drying, they obtain a typical brown color and can thereby be easily distinguished from the rather bright green *Saccoloma elegans* at any developmental stage. Interestingly, the color of *S. elegans* is identical to that of *S. inaequale* (Kunze) Mett. from western Amazonia, and seems not to be as dependant on the method of drying as the color of *M. rostrata*.

Because the present paper only deals with a limited number of species, the

identification key is not as complete as it ideally could be. At least in the genera *Campyloneurum* and *Elaphoglossum* there are several additional species that resemble the species included here so much as to create confusion. Because of the characteristic venation of *Campyloneurum*, specimens belonging to any species of this genus probably key out to the correct genus, but species identification should be checked with Tryon and Stolze (1993) or other sources. The situation is more difficult with *Elaphoglossum*, because in spite of great variation in almost all other characteristics, these species have parallel venation just like the majority of the species included in our key. Therefore other species of *Elaphoglossum* do not necessarily key out correctly to that genus, and in doubtful cases Tryon and Stolze (1991) should be consulted.

When sterile, *Thelypteris macrophylla* is rather similar to *T. lingulata* (C. Chr.) Morton both in size, general shape and venation. The diagnostic characteristics include the shape of the pinna base (cuneate to rounded in *T. macrophylla*, attenuate to cuneate in *T. lingulata*), the shape of the veinlets (almost straight in *T. macrophylla*, subsigmoid in *T. lingulata*) and the color of the dried leaves (brown in *T. macrophylla*, usually more green in *T. lingulata*). When fertile, these species are easy to tell apart because only *T. macrophylla* has acrostichoid sori. Also the growth forms are different: *T. macrophylla* is erect, whereas the leaves of *T. lingulata* are more hanging (Benjamin Øllgaard, personal communication). As we did not have juvenile material of *T. lingulata* available, it could not be included in the present study.

Another species group that had to be excluded due to lack of juvenile collections is *Polybotrya* subgen. *Soromanes*, which shows great resemblance to *Cyclodium meniscioides*. Most of these species are montane, but *Polybotrya polybotryoides* is also found in the lowlands and may easily generate confusion. Fortunately, the treatment of Moran (1987) includes good illustrations of the venation patterns in both species, and can be consulted to confirm the identification.

Among the species treated here, the venation of *Bolbitis nicotianifolia* is easy to tell apart. However, it is relatively similar to the venation of *Tectaria incisa* Cav.. The most obvious difference between these two is the rhizome. *Tectaria incisa* is always terrestrial and has an erect, cylindrical, very compact rhizome, whereas *B. nicotianifolia* has a long-creeping dorsiventral rhizome, which especially in terrestrial individuals is very slender. The pinnae of *B. nicotianifolia* are entire and regularly rounded, while in *T. incisa* there is a strong tendency for the terminal pinna and the basal pinna pair to become lobed or asymmetric in shape. The petiole, rachis and midrib of *T. incisa* are densely covered by short, erect hairs at least on the adaxial side, whereas those of *B. nicotianifolia* are glabrous or with scattered, linear-lanceolate scales.

It can be concluded that although the juveniles of species belonging to different genera may in some cases be rather similar, in other cases the differences in juvenile development of closely related species may help to resolve taxonomical problems and phylogenetical patterns (cf. Hennipman, 1977). Therefore it will be an advantage if juvenile material become more widely available

in herbaria, allowing descriptions of juvenile forms to become more often included in systematic treatments.

ACKNOWLEDGEMENTS

We thank Josephine Camus, Robbin C. Moran and Axel Dalberg Poulsen for help in identifying the species, Robbin C. Moran and Benjamin Øllgaard for constructive comments on the manuscript, and Kalle Ruokolainen for testing the identification key. The herbaria AAU, BM, K, TUR and U are acknowledged for making their material available for study. Most of the voucher specimens used were collected during field work financed by the Academy of Finland and FINNIDA, and the preparation of this article was made possible by an EU exchange grant (Erasmus) to ATG.

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